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Population Structure, Distribution, Life Cycle and Reproductive Strategy of *Spilocuma watlingi* Omholt and Heard, 1979 and *S. salomani* Watling, 1977 (Cumacea: Bodotriidae) from Coastal Waters of the Gulf of Mexico

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POPULATION STRUCTURE, DISTRIBUTION, LIFE CYCLE AND REPRODUCTIVE STRATEGY OF *Spilocuma watlingi* OMHOLT AND HEARD, 1979 AND *S. salomani* WATLING, 1977 (CUMACEA: BODOTRIIDAE) FROM COASTAL WATERS OF THE GULF OF MEXICO.

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ABSTRACT: Populations of *S. watlingi* and *S. salomani* in Gulf of Mexico coastal waters south of Dauphin Island, Alabama were systematically sampled from July 1984 to June 1985. *Spilocuma watlingi* inhabited protected estuarine water of Pelican Bay, while *S. salomani* was only found seaward of the barrier bar-island system that separated Pelican Bay from the Gulf of Mexico. Both species were present throughout the year. *Spilocuma watlingi* was most abundant in autumn and winter and had a single winter reproductive peak, but fecundity was low. Abundance and reproductive peaks for *S. salomani* were not determined because samples were not collected during the winter months and, when collected, too few specimens were obtained. Mature males in both populations were the smallest individuals. Intermediate in size between mature males and females was a non-sexually dimorphic stage. Preparatory and gravid females were the largest individuals and their numbers were at least twice that of males. A protandrous reproductive strategy is proposed where small mature males metamorphose into intersex stages which then become females.

Cumaceans, a group of infaunal crustaceans inhabiting benthic substrates from estuaries (Vader & Wolff, 1973) to abyssal depths (Jones & Sanders, 1972), are quite diverse in the waters along the Alabama coast of the Gulf of Mexico (Modlin & Dardeau, 1987). A limited amount of ecological information is availbale for some species inhabiting this coastal region. Abundance, distribution and life history data for *Cyclaspis varians* Calman 1912, *C. pustulata* Zimmer 1943, *Oxyurostylis smithi* Calman 1912, and *Mancocuma alterum* Zimmer 1943 (probably a *Spilocuma* sp.) from the Gulf waters off Mississippi were presented by Weaver (1974). Saloman (1981) described the ecology of *S. salomani* inhabiting the coastal water off northwestern Florida. Modlin and Dardeau (1987) examined seasonal and spatial distributions of *O. smithi, Leucon americanus* Zimmer 1943, *C. varians, Eudorella monodon* Calman 1912 and *Almyracuma proximoculi* Jones and Burbanck 1959 in Mobile Bay, Alabama, and recently Stearns and Dardeau (1990) added to the information known about *A. proximoculi*. The life history of *A. proximoculi* was examined in a population inhabiting coastal western Atlantic waters (Duncan, 1983, 1984).

Specimens from the coastal waters off Mississippi identified by Weaver (1974) as *Mancocuma alterum* probably belong to the genus *Spilocuma*. Weaver's description superficially compares to the descriptions of Omholt and Heard (1979) and Watling (1977). Additionally, the habitats in which Weaver collected his specimens were very similar to those found in Pelican Bay (Fig. 1). A recent survey by Rakocinski et al. (1991) in the habitats Weaver sampled produced only *Spilocuma* spp.

This paper presents information on the seasonal and spatial distribution, population structure, fecundity and life cycle of *S. watlingi* and *S. salomani* from coastal Gulf of Mexico waters south of

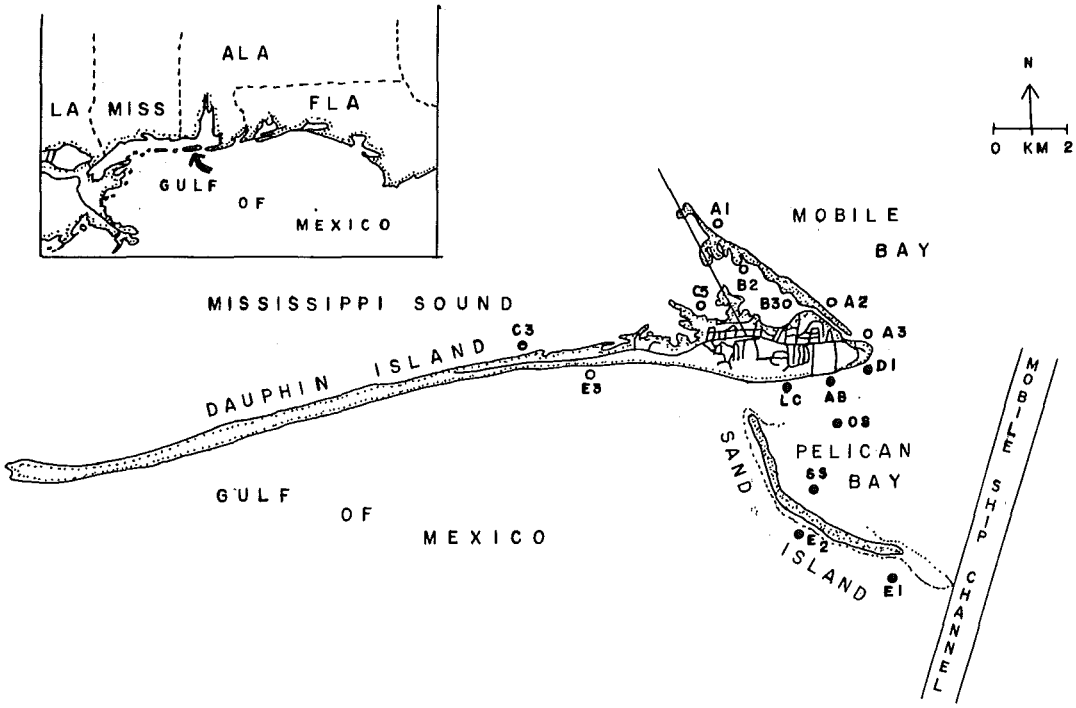

Figure 1. Location of the collecting sites in the waters surrounding Dauphin Island, Alabama. Black circles indicate collecting sites visited monthly and open circles irregularly sampled collecting sites. Arrow in inset shows the position of Dauphin Island along the Alabama Gulf of Mexico coast.

Dauphin Island, Alabama. The typical habitat of *S. watlingi* was orignally described as protected mesohaline waters in the vicinity of Dauphin Island (Omholt and Heard, 1979), while that of *S. salomani* was the high energy community off Panama City Beach, Florida (Watling, 1977).

MATERIALS AND METHODS

Populations of *S. watlingi* and *S. salomani* were systematically sampled at five stations (depths ranged from 0.5 m to 3.0 m) located in Pelican Bay and two off the seaward coast of Sand Island (depth ranged from 1.5 m to 2.0 m) (Fig. 1). Pelican Bay stations were sampled monthly from July 1984 to June 1985. Likewise, collections seaward of Sand Island were made monthly except in November, December and January when extremely strong longshore currents and heavy seas were prevalent. Specimens of *S. salomani* collected at the seaward stations E1-E3 were pooled because so few specimens were collected. To determine spatial distribution qualitative samples were irregularly collected in other locations around Dauphin Island and in Mobile Bay (Fig. 1).

Collections were made with an epibenthic dredge constructed from a 1.0 deep Nitex bag (mesh = 0.5 mm) attached to a 0.5 m wide by 0.1 m high rectangular metal frame with a pair of upward directed handles. With the aid of SCUBA, the epibenthic dredge was pushed along a 10 m transect delineated by a nylon line. The diver anchored one end of the line, held the other end, and swam into the current pushing the dredge until the line became taut. The epibenthic dredge effectively sampled the upper centimeter of sediments and the bottom nine centimeters of water column. When the sample was collected, the epibenthic dredge was closed by folding the frame

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back onto the net. The epibenthic dredge was then carried to the surface and its contents washed into a sample jar.

Samples were immediately fixed in a 5.0% seawater-Formalin solution and stained with Phloxine B to facilitate sorting. All samples were later sorted, without subsampling, to taxa and preserved in 70% ethenol. Cumaceans were additionally sorted to species, life stage and gender.

Measurement of total length, the distance from the anterior margin of the pseudorostrum to the posterior margin of the sixth pleonite, was made using an ocular reticule calibrated to a stage micrometer. All whole specimens were measured. Eggs of only those gravid females that appeared to contain full brood pouches were removed and counted.

Temperature and salinity of the surface and bottom water was measured at each sampling site with a YSI Salinity-Conductivity-Temperature meter using a remote probe. Depth of each transect was determined with a Dacor depth guage.

All satistical analyses were made using tests found in the ABSTAT Statistical Software package, Anderson-Bell Corporation, Parker, Colorado.

Description of Study Area

Pelican Bay (30°13′00″ N, 88°05′30″ W) is a shallow body of water strongly influenced by the hydrodynamics of Mobile Bay (Schroeder & Lysinger, 1979; Schroeder, et al., 1985). The study area south of Sand Island is a high energy beach community exhibiting the marine characteristics of the open Gulf of Mexico. It is separated from Pelican Bay by Sand Island and a submerged barrier bar (depth <1.0 m) that extends in a northwesterly directed arc from the Mobile Bay ship channel to Dauphin Island (Fig. 1). A 5.0 m deep, narrow (<1.0 km) channel separates the western end of the barrier bar from Dauphin Island. Pelican Bay-Sand Island barrier system is considered an ebb tide delta region; on an ebbing tide water from Mobile Bay flows westward around the eastern tip of Dauphin Island and strongly influences Pelican Bay water (Schroeder, Personal Communication). During the ebbing tide Pelican Bay, especially during periods of high river discharge, exhibits estuarine conditions. Additionally, the Mobile Bay signature is reflected in the sediment compositon of Pelican Bay. Sediments are composed predominantly of silt, clay and sand, with very transient surface material. Pelican Bay sediments, in addition to being 8.0% to 14% sand, are recently deposited clays and silts transported seaward during high river discharge and eroded clays characteristic of sediments reflecting the paleogeology of the Mobile Bay system. Isphording and Elliot (1979) and Modlin and Dardeau (1987) described the sediments of Mobile Bay. Sediment composition south of Sand Island is primarily clay, sand and gravel.

During the study period salinity and water temperature in Pelican Bay fluctuated seasonally and with the tidal cycle. Over the study year salinity averaged 20.0 ‰ and ranged from 31.5 ‰ in August to 7.1 ‰ in Feburary. Water temperature in Pelican Bay averaged 24.3° C during the study year and ranged from 11.9° C in February to 32.0° C in August. Salinity off Sand Island averaged 25.9 ‰ (range 22.5 ‰ - 28.8 ‰), and temperature averaged 27.8° C (range 25.0° C - 35.5° C). Wave action in Pelican Bay ranged from 0.3 to 1.0 m; currents were moderate and of tidal origin. Off Sand Island waves ranged from 0.5 to 2.5 m in height, in addition to tidal currents, high wave action generated extremely strong longshore currents. Underwater horizontal visibilty was 0.0 to 1.0 in Pelican Bay and 0.3 to 2.0 m south of

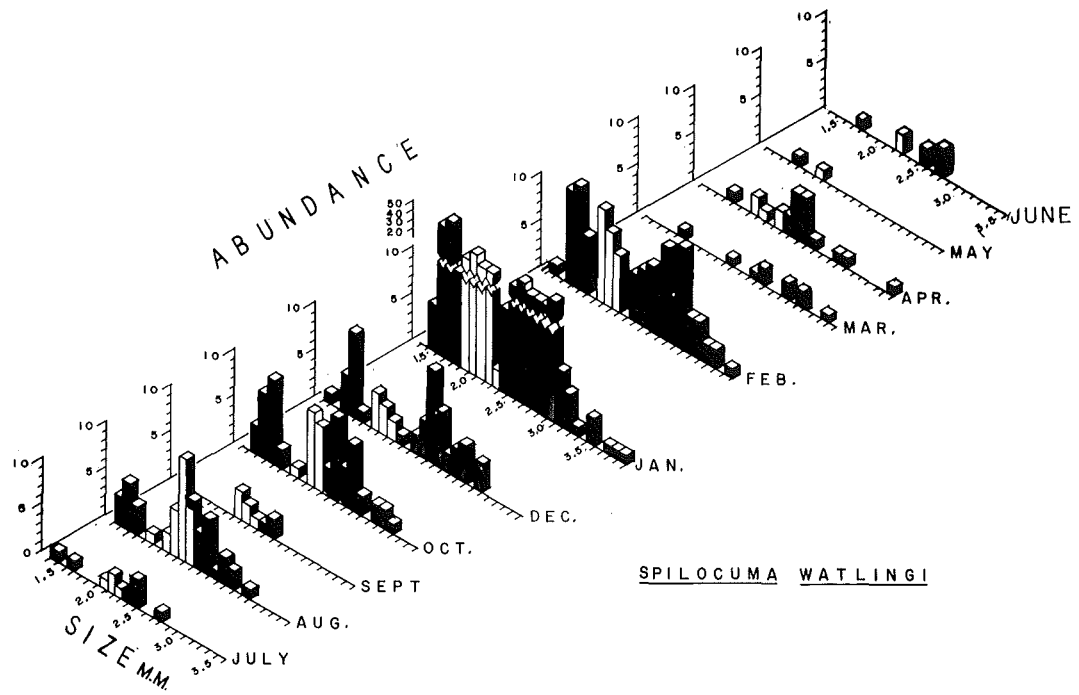

Figure 2. Total length frequency distribution for *Spilocuma watlingi* determined with individuals collected in Pelican Bay, Alabama study area during the study period from July 1984 to June 1985. Darkly shaded columns designate males, white columns intersex stages, and lightly shaded columns females. Abundance = number of individuals/m².

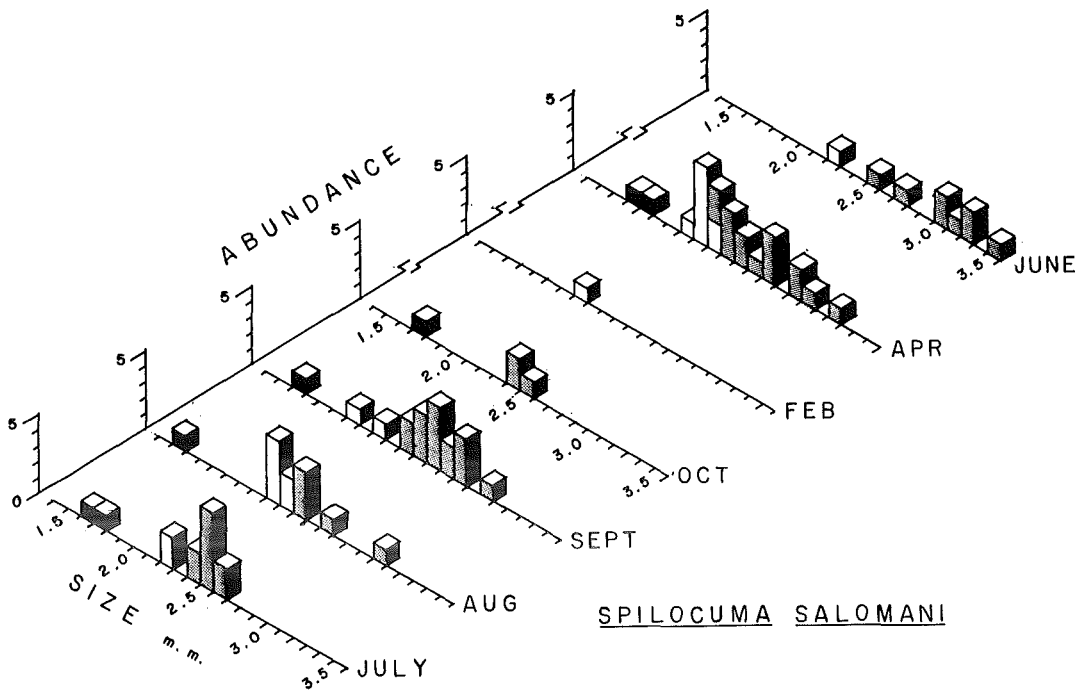

Figure 3. Total length frequency distribution for *Spilocuma salomani* determined with individuals collected in the study site south of Sand Island, Alabama during the study period from July 1984 to June 1985. Darkly shaded columns designate males, white columns intersex stages, and lightly shaded columns females. Abundance = number of individuals/m².

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Sand Island. The associated benthic fauna in the study areas is rich in polychaetes, crustaceans and molluscs (Vittor, 1979; Heard, 1982; Modlin, 1982; Modlin & Harris, 1989). Nekton of the area has been cataloged by Swingle (1971) and Shipp (1988).

RESULTS

In the waters surrounding Dauphin Island, Alabama *S. watling* and *S. salomani* occurred south of the island (Fig 1.). The *S. watlingi* population was found in the protected waters of Pelican Bay, while that of *S. salomani* was exclusively in the high energy, exposed beach community facing the Gulf of Mexico. Specimens of *S. watlingi* were obtained at all stations in Pelican Bay, but 95.4% of these were collected as stations DI, AB, and LC at depths <2.0 m (Fig. 1). Station (depth 1.7 m - 2.0 m) yielded only 2.0% of the total *S. watlingi* collected during the study period, while only 2.4% were obtained at station OS (depth 2.5 m - 3.0 m). Two specimens were collected at station E2 off Sand Island. From December through January, 98% of all *S. watlingi* were collected at station DI where depths ranged from 0.5 to 1.1 m.

Density of *S. watlingi* averaged 6.5 individuals/m^2. The population increased in numbers through autumn to a peak of 61.6/m^2 in Jaunary (Table 1). Thereafter, abundance decreased to a low in May and June. Average population density of *S. salomani* was 2.4 individuals/m^2. Because of the inability to sample the southern most sections of the study area, the size of this species' winter population was not determined. However, densities obtained in July, August, September, April and June were comparable to those measured for *S. watlingi* during those same months (Table 1). The single February specimen of *S. salomani* (Table 1) was collected at station E3 (Fig. 1).

The size frequency distributions for *S. watlingi* obtained during the study period are shown in Figure 2. and those for *S. salomani* in Figure 3. Manca stages were not collected. Males of both species were the smallest individuals; sizes ranged from 1.4 mm to 1.8 mm. They were present in both species' populations during the entire study period (Figs. 2 & 3). Males of *S. watlingi* were most common during the autumn and winter months (Fig. 2).

Developing ostegites were evident on all individuals 2.3 to 2.4 mm in total lenght (Figs. 2 & 3). Consequently, all individuals of these size classes and larger were considered females. In the population females occurred in a mixture of immature, gravid and spent life stages. Females of *S. watlingi* ranged in size to 3.9 mm, while those of *S. salomani* ranged to 3.5 mm. There was no progressive increase in size toward maturity. Immature and spent females occurred at a variety of intermediate sizes. Gravid females of *S. watlingi* averaged 2.9 mm and ranged from 2.6 mm to 3.6 mm in total length. Only two gravid females of *S. salomani* were collected; both were 3.2 mm in total length. Both specimens were collected in the spring.

A range of sizes intermediate between males and females did not show any secondary sex characteristics. These were considered to be an intersex stage. They were present in both species populations during the entire study period (Figs. 2 & 3).

Throughout the study period, females of both species outnumber males. Females of *S. watlingi* were on the average 4 times more abundant than males (Table 1). However, when the population was increasing in density from late summer through winter, the female to male ratios averaged 2:1. Males were very sparse in the population from March through June (Fig. 2). Female to male

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Table 1. Total abundance, male to female ratios (M:F) and male plus intersex to female ratios (MI:F) determined during the study period, July 1984 to June 1985, for the *Spilocuma watlingi* and *S. salomani* from the waters south of Dauphin Island, Alabama.

Month	Number/m²	M:F	MI:F
	Spilocuma watlingi		
July	2.2	1:2.0	1:0.6
Aug.	11.2	1:1.8	1:0.6
Sept.	1.8	—	—
Oct.	13.4	1:1.5	1:0.8
Dec.	12.6	1:2.1	1:1.1
Jan.	61.6	1:1.7	1:1.0
Feb.	22.0	1:1.9	1:1.0
Mar.	2.0	1:9.0	1:9.0
Apr.	4.4	1:16.0	1:2.7
May	0.4	—	—
June	1.6	1:5.0	1:1.7
	Spilocuma salomani		
July	2.6	1:4.0	1:2.2
Aug.	2.4	1:5.0	1:0.7
Sept.	3.6	1:1.0	1:3.0
Oct.	0.8	1:3.0	1:3.0
Feb.	0.2	—	—
Apr.	5.0	1:7.0	1:0.7
June	1.8	—	—

ratios for *S. salomani* ranged from 1:1 in September to 7:1 in April (Table 1).

Preparatory females were present in both species populations through the study period. However, peak reproduction in the *S. watlingi* population occurred during the months of December, January and February, when all life stages were in greatest abundance (Fig. 2) and gravid females comprised 10% of those collected. Two additional gravid females were collected at the end of summer. A least squares regression equation between total length and number of eggs or embryos indicated that an average sized *S. watlingi* gravid female carried 9 eggs. This regression followed the linear relationship $Y = 16.6X\text{-}39$. where Y is the number of eggs carried by a female of total length X; the correlation coefficient $(r) = 0.78$, sample size (n) $X = 16$. One gravid specimen of *S. salomani* carried seven embryos, while the other possessed three eggs. Neither of their brood pouches was full.

DISCUSSION

In the waters south of Dauphin Island, populations of *S. watlingi* and *S. salomani* have considerable opportunity to mix. They are found in contiguous habitats that are barely separated by a low island-shallow shoal barrier system (Fig. 1). Nevertheless, during the study period the populations remained separated. *Spilocuma salomani* was limited to the seaward exposed beach side of the barrier system and the unprotected western end of Dauphin Island (Fig. 1). Sediments in this community are composed of clays, sand and gravel (Isphording & Elliot, 1979). This habitat is identical to that described by Saloman and Naughton (1978) and Saloman (1981) for this species off the Florida Gulf of Mexico coast and by Rakocinski et al. (1991) off the Mississippi coast. Specimens of *S. watlingi* came from the type habitat described by Omholt and Heard (1979). *Spilocuma watlingi* prefers protected water areas where bottom sediments are composed of fine, poorly sorted grain sizes (Rakocinski et al., 1991). Like other cumacean species (Corey, 1970; Modlin & Dardeau, 1987, *S. watlingi* and *S. salomani* appear to have specific habitat preferences.

Seasonal distribution of *S. watlingi* is similar to other mesohaline species found in Mobile Bay (Modlin & Dardeau, 1987). The peak in abundance occurred in winter (Table 1), the period when salinities in the Mobile Bay estuary are normally highest (Schroeder, 1979). However, during February of the study year salinities in Mobile Bay had dropped to $7^{0}/_{00}$ (Dardeau, personal communication) and *S. watlingi* was still abundant (Fig. 2). Vargas (1989), from his work with *Coricuma nicoyensis*, suggested that salinity is an important environmental factor influencing the abundance of tropical Cumacea. *Coricuma nicoyensis* was most

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abundant at the highest salinities and lowest during the tropical rainy season when salinities are the lowest (Varga, 1989). Likewise, Modlin and Dardeau (1987) found salinity to be the key factor influencing seasonal distribution of Mobile Bay cumaceans. The low salinity observed in Mobile Bay during February 1985 was probably limited to the upper water column and, consequently, had little effect on the cumaceans which were closely oppressed to the bottom where salinity remains the highest. Saloman (1981) found that *S. salomani* had its greatest abundance along the Florida Gulf of Mexico coast during the spring months. Since no winter data were obtain for this species during this project, the timing of its peak in abundance in the study area is not known.

Both *Spilocuma* spp. appeared to breed continuously at low levels throughout the year, have one major peak period and low fecundity. *Spilocuma watlingi* had a reproductive peak in winter (Fig. 2) with an average fecundity of 9.0 eggs/female; *S. salomani* females produced an average of 6.7 eggs/female during their breeding peak in spring (Saloman, 1981). Corey (1984) found that *S. salomani* brood pouches contained an average of 31.1 eggs/female; a fecundity higher than determined by Saloman (1981) and that determined for *S. watlingi*. The reproductive cycle of *Dyastylis rathkei* was found to be retarded in years with severely low winter temperatures (Rachor et al., 1982). In the lower latitudes where salinity appears to influence cumacean dynammics (Modlin & Dardeau, 1987; Varga, 1989), this environmental factor may, like the influence of temperature in higher latitudes, also have a significant affect on reproductive cycles. Salinities were lower during the study year than in the previous and following years (Modlin & Harris, 1989).

The reproductive strategy of the two *Spilocuma* spp. is similar to that of *Pseudocuma longicornis. Pesudocuma longicornis* breeds continuously and has a low fecundity (Corey, 1981). However, it differs slightly because the smallest (1.4-1.8 mm) individual collected were mature males; no manca or juvenile stages (within the size range of the males) were collected. This suggests that brood pouch larvae are released at an advanced stage (Corey, 1984) — as mature males. Males are the smallest individuals (Figs. 2 & 3). Intermediate in size between mature males and females are individuals that do not show any sexual dimorphism. Consequently, the results of this study suggest that the repoductive strategy of the *Spilocuma* spp. may be protandrous. Brood pouch larvae develop directly into mature males. Once the males accomplish their task, they metamorphose into an intermediate sized intersex stage. Because of the range in total length, the intersex stages must pass through at least one moult before they show any female characteristics (Figs. 2 & 3). The range in female total lengths (Figs. 2 & 3) suggests that females pass through several moults. Since immature and spent females occur in sizes intermediate between gravid stages, females, at least in the winter months, can potentially produce several clutches of offspring during their lives.

An alternate to protandary suggested that the high activity of *Spilocuma* males results in their low numbers. This activity increases their exposure which makes them more available as prey or dispersed by unfavorable water currents (Saloman, 1981). Little evidence for this scenario exists.

In most dioecious reproductive strategies the female stage is derived from approximately half of the juveniles, with the other half becoming males. Consequently, allowing some loss to mortality and dispersal, the number of juveniles

should be about equal to, or greater than, the sum of the number of males and females. This condition is usually realized when dioecious populations are at maximum size; male to female ratios usually approach unity at this time. This is not the case with the two species here studies (Table 1). On average the females of *S. watlingi* outnumber the males by a factor of four (Table 1)). Saloman (1981) found similar results with *S. salomani*. However, the size structure data suggest a protandrous strategy where males of *Spilocuma* develop into an intersex stage which then molts into females. Therefore, the female component of the population is derived from the males plus the intersex stages. Again allowing for loss due to mortality and dispersal, a ratio between the numbers of male-intersex component and the numbers of females should approach unity. For *S. watlingi* during the interval from October through February, when the population was the largest (Fig. 2), the male-intersex to female ratio averaged 1:0.0 (range 1:0.8 to 1:1.1) (Table 1).

Protandry is not an unusual reproductive strategy among other Peracarida (Steele, 1962; Thomas & Barnard, 1983, Schram, 1986). Consequently, to find that protandry may occur in the Cumacea would not be unexpected. A protandrous reproductive strategy would also account for the loss of males from the population. Saloman (1981) suggested that in *S. salomani* males were a terminal pelagic instar stage and attributed their paucity in the population to predation and disperal. He did not distinguish an intermediate intersexual stage between males and females, nor did he produce a size frequency distribution for *S. salmoni* which would have brought the anomaly to light. However, to substantiate protandry in *Spilocuma* requires histoloical examination which has not yet been done.

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